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XVII. On the Organs of Voice in Birds. By William Yarrell, Esq. F.L.S.

Read June 2 and 16, 1829.

THE very liberal manner in which the Linnean Society did me the honour to illustrate a former paper on the Tracheæ of Birds, has been an additional inducement with me to render this subject as complete as my means of observation would allow: I therefore now submit descriptions and figures of the numerous muscles attached to the different parts of the windpipes of birds, by the action of which their varied and extraordinary powers of voice are produced, with representations of the tracheæ of four birds, which, though not all entirely unknown, are each of them illustrative of a portion of this subject, and have not been hitherto so represented as to afford a correct idea of their local situation or peculiarities.

The organ of voice in birds may be considered as consisting of four parts; the glottis or superior larynx, the tube of the trachea, the inferior larynx with its muscles, and the bronchiæ; and the variety of modulation birds are known to possess has its corresponding variety of forms. The glottis or superior larynx opens into the mouth at the root of the tongue. The orifice is long and narrow, encircled by two pair of muscles which govern the size of the aperture, and constitute one of the accessory means by which the sound of the voice is regulated. Birds have no epiglottis or covering over this aperture to prevent any 2 r 2 particles

particles of food passing into the windpipe; but the surface near the opening is furnished with numerous papillæ, pointing backwards, which assist in directing and conveying food towards and into the œsophagus.

TAB. XVII. Fig. 1. is a representation of the glottis with its surrounding membranes. Fig. 2. is a representation of the cartilages forming the superior larvnx. The letters, a, a refer to the principal cartilage, which, when in its natural situation, lies upon the pharyngeal portion, and between the cornua, of the os hyoïdes or bone of the tongue. This cartilage appears to perform the double office of the thyroid and cricoid cartilages in the higher animals. In substance it is uniformly thin, its shape nearly triangular, one angle placed forwards, the lateral angles curving upwards to support the base of the arytenoid cartilages on its own side. The letters b, b refer to the arytenoid cartilages, supported at their base by the lateral angles of the cricoid cartilage before mentioned, and projecting forwards in two narrow and thin parallel processes over two-thirds of the orifice formed by the curved lateral portions of the cartilage underneath : each parallel process forming a slight groove on its superior surface by the edges curving upwards.

The glottis is closed by a pair of muscles, (TAB. XVII. Fig. 4, a, a) extending from the upper portion of the cricoid cartilage along the crura of the arytenoid cartilages, upon each outer edge of which they are inserted; and it is opened by a pair of muscles arising from the lateral and posterior portions of the cricoid cartilage, the fibres of which passing over the pair of smaller muscles just described, are inserted upon the inner edge of each arytenoid cartilage (Fig. 3, b, b). The obvious use of these two pair of muscles is to govern the size of the aperture. Baron Cuvier in his Leçons d'Anatomie Comparée, vol. iv. p. 490, says, "Birds have no arytenoid cartilages;" but the uses

uses to which the two processes already described are subservient, and the action and effect of the muscles attached to them, render it difficult for me to speak of them under any better designation.

The tube of the windpipe is composed of two membranes, inclosing between them numerous cartilaginous or bony rings, forming a cylinder more or less perfect from end to end. Ossification appears to commence in these rings at the front of the trachea, from which point the bone gradually extends equally on both sides towards the œsophagus as the bird increases in age: in particular parts, however, of the tracheæ of some birds the rings are not entirely complete at any age. Various inequalities of size occur in different parts of the same tube in some species, producing, as might be expected, a particular effect on the voice, to be hereafter explained; and the length of the tube deserves consideration. Thus, shrill notes are produced by short tubes, and vice versa; the first are possessed by the Singing Birds, and the reverse by the Waders and Swimmers; but the diameter of the tube has also its influence, large tubes producing notes low in the scale, and vice vers \hat{a} . The substance of the tube itself has also to be considered, though some anomalies present themselves. Those birds possessing strong and broad cartilages or bony rings have monotonous and loud voices, while the more slender rings with enlarged spaces between them allow a freedom of motion producing a corresponding variety in the scale of tone.

The inferior larynx, the true situation of the organ of voice in birds,—as the experiments of Baron Cuvier have sufficiently proved,—is situated at the bottom of the tube, and is formed sometimes by the approximation of several of the lower rings of the trachea more or less firmly ossified together, and occasionally of solid bones; varying in form, being compressed, conical, cal, or triangular at its lower surface, (TAB. XVII. Fig. 7, 11, & 12) having a central cross-bone extending from behind to the front, dividing the orifice in two equal parts (Fig. 11 & 12, a,a); to the outer side of which cross-bone the inner membrane of each bronchial tube is attached. This cross-bone thus dividing the lower orifice, forms the point of divarication from which the bronchiæ arise separate, and go off to the lungs. But a more minute description of this important part will be given, when considering the various muscles connecting the bone of divarication with the bronchiæ.

The bronchiæ are formed on the outer sides by membrane interposed between and connecting a variable number of cartilages which describe only parts of circles, diminishing in size as they approach the lungs, the circle being completed on the inner side by a delicate membrane stretching from the opposite points of the semicircular cartilages, and forming a tube from the orifice of the inferior larynx to the substance of the lungs (TAB. XVII. Fig. 9 & 10, c, c). This membrane is called by Cuvier the membrana tympaniformis, and upon its dilatation and contraction, as well as the power afforded of altering the form and length of the bronchiæ, some of the varieties of intonation depend. The bronchiæ are also slightly attached to each other and to the æsophagus.

The muscles of the glottis or superior larynx are uniformly two pair in all the birds I have examined : but the muscles of the inferior or true larynx, all largely supplied with nerves, vary from one pair to five pair, according to the genus or species, affording a corresponding increase in the various qualities of the voice. Some few birds have no true muscles of voice at the inferior portion of their tracheæ. Cuvier describes the King of the Vultures as being without any ; and this is also the case with the Condor. TAB. XVII. Fig. 5. is a representation

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of the lower portion of the trachea of a Condor Vulture without muscles or any true bone of divarication, the bronchial rings almost completing the circle, with little flexibility, and the voice of the bird monotonous. The want of muscles of voice will be more immediately apparent by comparing this representation with those of TAB. XVIII. all of which exhibit various muscles attached. The Spoonbill is another instance of a bird without any true muscles of voice. TAB. XIX. is a representation of part of the inside of this bird with the convolutions of its singular trachea in situ: the insertion of the bronchiæ into the lobes of the lungs is shown, but no ossification at their junction with the tube of the trachea will be observed, nor any muscles by which variations in the length of the trachea or bronchiæ can be effected. The convolutions of the trachea of the Spoonbill have been described, but I am not aware that they have been figured.

The next division, or those birds possessing one pair of muscles of voice, is by far the most numerous, including as it does the genera Falco and Strix, some of the Insessores, all the Rasores, Grallatores, and Natatores, with a few exceptions only, which will be pointed out. I refer particularly to the British species of these different orders, as it is with them I am best acquainted.

The single pair of muscles with which these birds are provided, arise from the whole outer surface of the cricoid cartilage; descending, they form a sheath round the upper part of the tube, afterwards dividing and passing downwards in two equal portions, one on each side, uniformly attached to the tube, and not quitting it till arrived at or near the bone of divarication; when, separating from the tube, they pass outwards and downwards in distinct slips on each side to be inserted upon each inner lateral edge of the sternum. This pair of muscles support

support the trachea, and serve to accommodate the tube to all the varied inflexions of the neck : they influence the length of the trachea as well as that of the bronchiæ, and on account of their place of insertion have been named sterno-tracheal.

TAB. XVIII. Fig. 1. & 2. are a front and side view of a trachea furnished with one pair of muscles, in which the letters d, dmark the portion of each muscle going off to be inserted upon the sternum. TAB. XX. Fig. 1. represents the trachea of the Curassow (*Crax Alector*) with its singular convolution lodged between the shafts of the os furcatorium. Fig. 2. represents the posterior aspect of the same trachea removed from its natural situation to show its single pair of muscles (d, d).

Some of the birds possessing two pair of true muscles of voice may be considered as exceptions to a general rule, rather than otherwise, since they belong to those orders which usually possess but one pair.

The Indian Crowned Pigeon, the largest example of the family, exhibits this second pair of muscles (TAB. XVIII. Fig. 3, e). They are formed of a portion of the sterno-tracheal muscles, but taking a different direction. They proceed by a narrow slip, from that point upon the tube where the first pair of muscles go off to be inserted upon the sternum, down the side of the trachea, to be attached externally to the membrane between the lowest ring of the tube and the first ring of the bronchia, as shown in the side view before referred to. By their contraction they shorten the flexible portion of the tube between their points of attachment, and produce tension upon the membrana tympaniformis. Our British Pigeons exhibit a few fibres in the same relative situation.

The Wood Grouse is remarkable for its variation in the organ of voice from other Gallinaceous birds. The tube of the trachea is one fourth longer than the neck of the bird, and this excess forms

forms a free and loose curve or fold within the skin (TAB. XXJ. Fig. 1, a). The first pair of muscles of large size are not attached to the tube throughout any part of its length as in other birds (Fig. 1, d), but pass separately downwards, becoming connected together below the convolution of the trachea, and inserted upon the os furcatorium or merrythought, at the angle formed by the junction of the two shafts of that bone. About the commencement of the lower third portion of these muscles, each of them sends off a narrow slip downwards, which becomes attached on its own side to a strong membranous sheath that invests and strengthens the lower portion of the trachea (Fig. 1, e), ultimately quitting the tube above the point of divarication in the ordinary way, to be inserted upon the sternum, becoming the true sterno-tracheal muscles; the first pair, from their place of insertion, being called furculo-tracheal, of which we shall hereafter find further examples. TAB. XXI. Fig. 1, is a representation of the trachea and its muscles in this bird, in which another peculiarity will be observed. By the contraction of the first pair of muscles, marked d, the glottis may be drawn downwards two inches below its ordinary or true situation upon the pharyngeal portion of the os hyoides: the length and flexibility of the tube of the trachea itself, and the power of withdrawing the glottis just noticed, forming a considerable cavity by the elongation of the pharynx, are principally instrumental in producing the very powerful voice this bird is known to possess. The muscles for elevating and directing the glottis to its ordinary situation are also shown.

Among the *Natatores*, which I have stated generally as possessing but one pair of muscles of voice, there are four exceptions known; the Velvet Duck, the Golden-eye, the Red-breasted Merganser, and the Gannet; these birds possess a second pair of muscles of voice.

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The Velvet Duck is remarkable for a hollow bony enlargement in its trachea, situated about two-thirds down the tube, made up of expanded tracheal rings firmly ossified together. Upon each side of this enlargement a small muscle, marked *e*, arises, which, passing downwards, is inserted upon the inner side of the shaft of the *os furcatorium*, and the voice is probably influenced by the action of these muscles altering the relative situation of this hollow bulb upon the tube.

There is also another peculiarity, which, as far as I am aware, has not been noticed. On making a longitudinal section of the trachea of this rare British bird, (representations of the inner surfaces of both halves of which are shown at TAB. XXI. Fig. 2, & 3,) it will be seen, that the inner tube of the trachea at its upper part has an aperture on each side, by which it communicates freely with the cavity within the bony enlargement situated immediately below the superior larynx, and brings to mind the laryngeal cavities found in some of the higher animals. A slip of paper is represented as passing through both apertures. Letters d, d, represent the ordinary sterno-tracheal muscles.

In the Golden-eye, the second pair of muscles is of large size, and inserted also upon the shafts of the os furcatorium. They arise in part below, and upon a portion of the surface of the enlarged rings, which form the bulb on the tube of that bird. When the voice is not exercised, these enlarged rings lie folded flat upon each other, but by the contraction of these muscles, the rings are set up at right angles to the axis of the tube, and the air, forced through and vibrating in an enlarged hollow cavity, acquires a degree of power which has obtained for this bird the specific name *Clangula*.

The trachea of the Red-breasted Merganser has also a permanent enlargement of a portion of the rings, forming a bulb on the tube. It has also a second pair of muscles (furculo-tracheal), which which go off about half-way between this bulb and the inferior larynx, to be inserted upon the os furcatorium. These muscles are called ypsilo-tracheal by Baron Cuvier, from the form of the bone upon which they are inserted. They seem peculiar to those birds having enlargements of the tube, and figures of the two last-mentioned tracheæ will be found attached to Dr. Latham's Paper in the 4th volume of the Transactions of the Linnean Society.

I have mentioned the Gannet as differing from the Natatores generally in being provided with a second pair of true muscles of voice; but the second pair in this bird differ materially from the furculo-tracheal muscles already described as existing in the three species of palmated birds having enlargements of the tube. The trachea in the Gannet is uniform in size throughout, and furnished with one strong pair of muscles, which, passing down the side of the tube nearly the whole of its length, go off to be inserted upon the sternum as usual. Underneath and below these there is another pair given off from the inner surface of the first, which pass directly downwards, and are inserted upon the upper surface of a spherical glandular protuberance fixed to the upper or first half-circular bronchial cartilage. The membranous division between the point or bone of divarication and this first ring is considerable; and the contraction of this second pair of muscles shortens the bronchiæ the whole depth of this division, producing at the same time corresponding tension of the membrana tympaniformis. The protuberances upon the bronchiæ here noticed are solid, unctuous in appearance, and probably perform the office of bronchial glands. TAB. XVIII. Fig. 4, & 5, represent the lower portion of this trachea in two points of view.

Tracheæ possessing three pairs of true muscles of voice are confined entirely, as far as my observations have extended, to one very large family only, the *Psittacidæ*; and these muscles

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will be found uniform in situation and shape throughout the whole of the Parrot tribe. The upper orifice is governed by two pair of muscles as in other birds; and when mentioning the true muscles of voice, I refer only to those situated near the inferior larynx. As the organ of voice is more complex in these birds than in any of those hitherto noticed, it will be necessary to enter somewhat more into detail. The bony rings forming the tube of the trachea are strong, and of large size at the upper part, diminishing gradually as they approach the point of divarication, which is formed by the lower rings becoming elongated from before backwards, and terminating both before and behind in a small triangular-shaped bone (TAB. XVII. Fig. 8, b) having its apex pointing downwards. To each side of the bottom of the tube there is attached by intervening membrane a thin crescentshaped bone (TAB. XVII. Fig. 6, b), the horns of which, directed also downward, pass below the points of the triangular interposed bones; the connecting membrane permitting a certain degree of lateral motion in the inferior edges of both these crescent-shaped portions of bone. TAB. XVII. Fig. 6. 7. & 8, represent these parts as they appear when divested of their muscles in the great blue and yellow Macaw. None of the Parrot tribe possess the cross-bone which usually divides the opening at the bottom of the tube in other birds. The bronchiæ are triangular in shape and very short, extremely flexible, being made up principally of membrane with slender semicircular cartilages placed at considerable distances from each other, having a broad surface of membrane only between the lower edge of the moveable bones of the tube, and the first bronchial cartilage, to facilitate the requisite alteration in the length of the bronchial tubes. The inner membranes of the bronchiæ unite at their upper broad edges to form their own division between the bronchiæ in the absence of the cross-bone.

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The first pair of muscles after passing down the sides of the tube in the ordinary way do not guit it to be attached to the sternum, but have their tendons inserted upon the outside of the second pair of muscles, their use being to influence the length of the tube, and assist the second pair in their action upon the bronchiæ (TAB. XVIII. Fig. 7, d). The second pair of muscles have their origin one on each side a little above the bones of divarication. Somewhat broad at first, they become narrower as they pass downwards, and are inserted upon the outer and central portion of the bronchiæ at the fourth semicircular cartilage (Fig. 7, e). The third pair of muscles arise broad and thick from the sides of the last ring of the tube, and are inserted over the whole surface of the moveable crescentshaped bones below (Fig. 7 & 8, f), their obvious use being that of separating the inferior edges of these bones, thereby enlarging the aperture. Fig. 8. represents a side view of the lower portion of the trachea in the Macaw, the three muscles detached from each other to render them more distinct. It may be necessary here to remark that the two sides of a trachea and their attendant muscles are invariably alike, except in some of the Anatida. Fig. 6. & 7. are two views of the same portion of the trachea with the three pair of muscles in situ. Their different powers will be obvious on inspection; the second pair, marked e, performing by their contraction the double office of altering the length of the bronchiæ, and, pressing upon the projecting surface of the third pair of muscles, which they pass over, diminish the aperture formed by the edges of the moveable semilunar-shaped side bones. It is to this power of diminishing the aperture these birds are indebted for the notes they are able to produce so high in the scale of tone.

I have never yet been fortunate enough to meet with a bird possessing four pair of true muscles of voice. I proceed therefore

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to the consideration of the most complex organ, that furnished with five pair.

The birds included in this division are all the Corvi, Starling, Thrush tribe, Larks, Buntings, Finches, Warblers, Swallows, &c., the organs of voice in which vary only in size. The tube of the trachea is generally uniform in shape throughout, the bronchiæ long in proportion, and both parts perfectly flexible. TAB. XVIII. Fig. 9. 10. & 11. are an anterior, posterior, and side view of a portion of the trachea and its muscles in the Raven, which may be considered as the type of this form, and from its size admits of clear explanation. TAB. XVII. Fig. 9. is a side view of the same part divested of its muscles, to show by the prevalence and interposition of membrane the degree of alteration the various muscles are able to effect.

TAB. XVII. Fig. 10. represents part of the same trachea, one bronchia having been removed to show the membrana tympaniformis, letter c, on the inner side of the other. TAB. XVII. Fig. 11. is a view of the under surface of the bone of divarication. Letter a with a cross is the wider posterior part to admit the passage of the cosophagus from behind forwards, between the bronchiæ, when both are in their natural situation. Letters a, in Fig. 11. & 12. mark the situation of the crossbone.

Referring again to TAB. XVIII. Fig. 11. the pair of muscles which descend on the outside of the trachea, divide at a short distance above the end of the tube, and send one portion in continuation downwards and backwards, to be inserted upon the extreme posterior end of the first bone of the bronchia, and is marked f. Its counterpart (e) passes from the place of separation downwards and forwards, to be inserted below the extreme point of the last bone of the tube. Within the angle formed by the separation of these two muscles, a third slender and

and cord-like muscle (d) arises, which goes off to be inserted upon the sternum. The fourth muscle (h) is the shortest of the five, and partly hid by the muscle just described marked f. It arises near the centre of the bottom of the tube, and its fibres, directed obliquely backwards and downwards, are inserted by tendon upon the extremity of the first half-circular bone. The fifth muscle, marked g, arises also from the centre of the tube similar to the last, but is something longer, oval in shape, and much more fleshy. It has the appearance of being made up of several small muscles in close contact. Its direction is obliquely downwards and forwards, its substance in part hid by the muscle already described, marked e, and it is attached by a broad base to the last bony ring of the tube, to the cartilaginous projection immediately below, and sends one portion to be inserted upon the extreme end of the first bronchial bone. Fig. 12. represents these five muscles, three of them being partly detached for distinction. Should names for these four muscles be considered necessary, they may be called the long and short anterior and posterior tensors : the muscle, marked d, from its insertion upon the sternum, may still retain the name of sternotracheal. Thus, it will be seen, the lungs govern the volume of air as well as the force with which it is expelled, while these muscles influence the diameter and length of the bronchial tubes.

The advantageous size of the organ of voice in the Raven, and its perfect similarity to those of all the song-birds, was my reason for selecting it in illustration of a subject to which, in quality of tone, there is no resemblance; but it must not be forgotten that this bird possesses the power of imitating that most difficult of all sounds, the human voice.

It will appear anomalous that the Parrots, with their three pair of muscles of voice, should possess a greater range of sound,

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or compass of voice, than those provided with five pair; but it will be seen by a reference that the insertion of the principal muscle shortening the bronchial tube, in the Parrots is much lower down than in any other birds; nor do any of the songbirds possess the power of altering the size of the aperture at the bottom of the tube of the trachea. Considerable advantage is supposed to be afforded the Parrots by their soft, fleshy, human-like tongue; yet it cannot be denied that the Raven, Magpie, Jay and Starling produce a close imitation of the human voice with tongues long, slender and horny. The celebrated Mocking-bird of America, which I have once had an opportunity of examining, has an organ of voice and tongue precisely similar to our own Song-thrush.

The organs of voice in the Mammalia, possessing chordæ vocales, have been considered to bear some relation to musical instruments with strings; and those of birds, to wind instruments. Among the latter, (with most of which there are some points of similarity,) they appear to me to have a closer resemblance to the French horn than any other; the bronchiæ performing the same office as the lips of the musician, and the muscles of the glottis, like the hand, governing the extent of the other aperture. The voices of the Stanley Crane and Demoiselle, with their single convolution in the trachea, are lower in the scale of tone than those of the other species of the same family having no such convolution; and the Common Crane with his elongated double convolution possesses a voice still deeper than the Stanley Crane or Demoiselle. In this circumstance they also particularly resemble the French horn, the performers upon which fix additional circles of tube upon their instrument when required to take a part in any concerted piece of music that is set in a low key.

It will perhaps be objected, that the utmost extent of motion which

which birds appear to possess the power of exercising over the various parts of their organ of voice, seems insufficient to account for the effects produced; but it may in answer be urged, that the closest examination or most scientific demonstration of the chordæ vocales and muscles in man, with all the auxiliary appendages, afford but an imperfect illustration of the varied and extraordinary powers of the human voice.

EXPLANATION OF THE PLATES.

TAB. XVII.

- Fig. 1. The glottis in situ. a, a, a. Part of the pharynx. b. The rima glottidis.
 - Cartilages of the superior larynx. a, a, a. Cricoid cartilage. b, b. Arytenoid cartilages. c. Upper rings of the trachea.
 - 3. b, b. The muscles opening the arytenoid cartilages. a. Part of the muscle closing the arytenoid cartilages.
 - 4. Shows at a, a, the muscles closing the arytenoid cartilages.
 - 5. Part of the trachea of a Condor Vulture (Vultur Gryphus). a. Part of the tube. b. Point of divarication. c, c. The bronchiæ.
 - 6. Side view of the lower portion of the trachea of the Great Blue and Yellow Macaw (*Psittacus Ararauna*).
 a. Part of the tube. b. Semilunar bone. c. The bronchia.
 - 7. Bottom of the tube seen from below.

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- Fig. 8. Front view of the same trachea. a. Part of the tube.b. The triangular bone between the crescent-shaped bones.
 - Side view of the trachea of the Raven (Corvus Corax).
 a. Part of the tube. b. Point of divarication. c. Bronchia outside.
 - 10. Another view of the same, one bronchia being removed to show the inner portion (membrana tympaniformis) of the other, letter c.
 - Bone of divarication in the Raven (Corvus Corax), seen from below. a*. Posterior part. a, a. Cross-bone. b, b. The sides.
 - 12. Lower part of the trachea of the Great Black-backed Gull (*Larus marinus*). b. The triangular bone of divarication; and a, a. The triangular cross-bone.

TAB. XVIII.

- Fig. 1 & 2. Front and side views of a trachea having one pair of muscles of voice. a, b, & c. Refer as before. d, d. The first pair of muscles.
 - Side view of a trachea with two pair of muscles of voice.
 d. Sterno-tracheal or first pair. e. The second pair.
 - 4 & 5. Front and side views of part of the trachea of the Gannet (*Pelicanus bassanus*), having two pair of muscles of voice. d, d. The first pair, sterno-tracheal. e, e. The second pair.
 - 6 & 7. Front and side views of part of the trachea of the Great Blue and Yellow Macaw (*Psittacus Ararauna*), having three pair of muscles of voice. d, d. The first pair. e, e. The second pair. f, f. The third pair.
 - 8. Side view of the same, the muscles partly detached for distinction. Letters of reference the same. Fig.

- Fig. 9. 10 & 11. Front, back and side views of part of the trachea of the Raven (Corvus Corax). d. The sternotracheal muscle. e. The long anterior tensor. f. The long posterior tensor. g. The short anterior tensor. h. The short posterior tensor.
 - 12. Side view of the same trachea, the muscles partly detached for distinction. Letters of reference the same.

TAB. XIX.

Trachea of the Spoonbill (Platalea leucorodia) in situ.

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- Fig. 1. Trachea of the Curassow (Crax Alector) in situ, seen from before.
 - The same trachea seen from behind. a, a. The convolutions of the tube. b. Point of divarication. c, c. The bronchiæ. d, d. The single pair of muscles of voice.

TAB. XXI.

- Fig. 1. Trachea of the Wood Grouse (Tetrao Urogallus), half the natural size. a. The loose portion. c, c. The bronchiæ. d. The furculo-tracheal muscles. e, e. The sterno-tracheal muscles.
 - 2 & 3. Inside views of both halves of the trachea of the Velvet Duck (Anas fusca). d, d. Sterno-tracheal muscles. e, e. The furculo-tracheal muscles. a, a. The laryngeal cavity.

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